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NOMENCLATURAL STATUS OF THE PALAEOBOTANICAL "ARTIFICIAL TAXA" ESTABLISHED IN BRONGNIART'S 1822 "CLASSIFICATION" PAPER

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Abstract: Brongniart's 1822 paper "Sur la classification et la distribution des végétaux fossils" was one of the most important early contributions to palaeobotany, especially in its treatment of how to name and classify plant fossils. Twenty four genera / sections were named in this work. Seven of these names have been supressed for nomenclatural or taxonomic reasons (*Exogenites*, *Clatharia*, *Sagenaria*, *Filicites*, *Phyllites*, *Poacites*, *Carpolithes*), and four are difficult to use because of problems with typification and / or diagnosis of the taxa (*Endogenites*, *Culmites*, *Fucoides*, *Antholithes*). However, many of the remaining names are still in widespread use, albeit not always correctly, notably *Calamites*, *Sigillaria*, *Stigmaria*, *Sphenopteris*, *Neuropteris*, *Pecopteris*, *Odontopteris*, *Sphenophyllum*, *Glossopteris*, *Asterophyllites*, albeit with altered orthographies or conserved with different types.

Key words: Palaeobotany, fossil taxa, Brongniart

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Introduction

Scientific palaeobotany is normally taken to have started in the 1820s. Although there had been a number of earlier publications in the subject (reviewed by Andrews 1980) the works of Schlotheim (1820), Sternberg (1820–1838) and most significantly Brongniart (1822a–c, 1828a, 1828b–1838b) were the first to address seriously the problems of how to name and classify plant fossils. As a result, the International Code of Nomenclature (ICN – McNeill et al. 2012) Art. 13.1 takes the starting point for palaeobotanical nomenclature as 31 December 1820.

The present paper will review the generic and section names that were used by Brongniart (1822a, b). Although not the earliest of these works it has arguably been the most influential; the earlier Schlotheim (1820) study failed to define properly many of the taxa included (Kvaček 1982) and is now taken to pre-date the starting point for palaeobotanical taxonomy, whilst that of Sternberg (1820, 1821) was limited to describing just a few arborescent lycopsid and sphenopsid stems. Brongniart (1822a, b) either first used or first validly published a number of taxonomic names that are still extensively used in the palaeobotanical literature, albeit often incorrectly. Some of these problems have been resolved by the names being formally conserved in the ICN, but not all of them. In this paper we examine the formal status of each of the Brongniart (1822a, b) generic and section names, and summarise the types of fossil to which they can be legitimately applied. Given that an original copy of this paper is not always easy to obtain and the quality of the on-line version is relatively poor, we reproduce here Brongniart's original illustrations of the key taxa discussed.

In this paper, when the name Brongniart is used alone, it refers to Adolphe-Théodore Brongniart (*1801, †1876), the subject of this study; when his father Alexander Brongniart (*1770, †1847) is referred to, his full name is given.

Background to Brongniart's "Classification" paper

Brongniart published his 1822a–c paper when only 21 years old (Stafleu 1966). It was not intended to be a monographic study of plant fossils (he was to start that some seven years later – Brongniart 1828b) but was rather a summary of how, in his view, plant fossils should be classified given the inherent practical and taphonomic problems. In particular he examined the problem of how to name plant

fossils that could not be assigned to the families and genera of modern-day plants (Stafleu 1966). This problem partly arose, we now know, because many plant fossils are the remains of long-extinct groups that, even if we had the whole living organisms, could not be assigned to modern-day families and genera. For instance, the arborescent lycopsids that dominated large areas of the Late Palaeozoic tropical wetlands cannot be placed in a taxon of living plants below the rank of class (Thomas and Brack-Hanes 1984, Thomas and Bek in press). Moreover, many plant fossils are the remains of isolated leaves and stems that would be difficult to classify using criteria derived from reproductive structures even if palaeobotanists wanted to.

For such fossils, Brongniart (1822a, b) established a set of 19 what he later referred to as "genres artificiels" (Brongniart 1828a: 10), defined purely on the characters that could be observed in the fossils. These genera were grouped into four morphological classes: 1. Stems with recognisable internal structure; 2. Stems without recognisable internal structure, but which have distinctive outer surface; 3. Stems with attached leaves, or isolated leaves; and 4. Fructifications. Class 4 was regarded as so diverse that it was further divided into two orders, for seeds and flowers, although each order only contained one genus.

The implication of this approach was that he was classifying the fossils as separate entities from the plants from which they were derived. This was fundamentally different from the approach of Sternberg (1820) who tried to use the fossils to classify the original parent organism. Many palaeobotanists have striven to reconstruct whole living plants from the fossil record, and in a few cases this has been achieved; most notable among 19th century palaeobotanists who tried to do this was Grand'Eury (1877) who published several proposed plant reconstructs based on some exceptionally preserved late Carboniferous fossils from the Loire Coalfield in France. However, Brongniart (1822a, b) realised that the fossils that could be reconstructed into whole plants in this way were the exceptions not the rule. Today, emphasis is given to reconstructing whole plants, partly because of the perceived necessity of using such models in phylogenetic analysis (e.g. DiMichele and Bateman 1996). Brongniart, in contrast, was working in pre-Darwinian times when phylogeny was not considered a major issue. Palaeobotanists were instead mainly interested in determining the distribution of past vegetation and what this told them about ancient environments, and this is best determined by studying and naming the detached fragments that make up the vast bulk of the plant fossil record.

Subsequent palaeobotanists continued to study the taxa described by Brongniart (1822a, b, 1828a, 1828b–1838b), which became progressively better understood. For instance, fossil-taxa of ferns that initially were defined just through pinna morphology later had details of their reproductive organs discovered. Lycopsid taxa initially defined on the external morphology of stems, later had their internal anatomy described while some stems have been found with terminally attached cones. Such progress was of course beneficial to the science but resulted in problems with the taxonomic nomenclature.

If the circumscription of one of Brongniart's taxa was narrowed to take into account the new data, the less-well understood fossils would be excluded. A new taxon would then need to be created to accommodate these less-well understood taxa, which itself might subsequently be revised and narrowed in circumscription if its type became better known, resulting in a rolling system of taxonomic instability. The only alternative would be to retain Brongniart's original "artificial" taxonomic concepts, but then the taxonomy would not be fully reflecting knowledge of the systematic positions of the fossils, a position few palaeobotanists would find acceptable.

Various solutions to this problem were suggested. Many studying fern fossils adopted what was in effect a dual generic nomenclature. For instance, fern fossils named as *Pecopteris* (*Asterotheca*) *miltonii* (Artis) Brongniart would have foliage with a morphology corresponding to the fossil-genus *Pecopteris* (Brongniart) Brongniart and sori with a morphology and anatomy corresponding to the fossil-genus *Asterotheca* C.Presl. *Pecopteris* (*Acitheca*) *polymorpha* Brongniart would have similar, *Pecopteris*-like pinnae but sori corresponding to the fossil-genus *Acitheca* Schimper. Other, less well-understood fossil-species for which reproductive structures were unknown could just be assigned to *Pecopteris*, such as *Pecopteris bucklandii* Brongniart This system had much merit because of its flexibility and was used extensively, especially in studies of Palaeozoic ferns (e.g. Kidston 1884, 1923-1925); and an attempt was made to incorporate it into the "Rules of Botanical Nomenclature" (Jongmans et al. 1935). However, it was eventually rejected and not included in the first "International Code of Botanical Nomenclature" (ICBN), probably because the resulting trinomial nomenclature may have caused confusion among those more familiar with the taxonomic nomenclature of living plants: for instance, *Pecopteris* (*Asterotheca*) *miltonii* might be taken to imply that *Asterotheca* was a subgenus of *Pecopteris*, an implication that was not intended.

Nevertheless, the "genres artificiels" introduced by Brongniart (1822a) continue to be used extensively by palaeobotanists, despite the fact that a strict application of the ICN means that their meanings have often changed substantially. For instance, many palaeobotanists continue to use the name *Pecopteris* for ferns with dentate pinnules but for which reproductive structures are unknown, despite (as we will show later) its type (*Pecopteris penniformis* (Brongniart) Brongniart) belonging to a much more narrowly defined genus, often referred to as *Senftenbergia* Corda. As a result, most palaeobotanists have tended to ignore the formal nomenclatural status of Brongniart's "genres artificiels" – in effect hoping that, by not talking about the problem, it would go away.

But provided taxonomic nomenclature continues to be based on the ICN, the problem will not go away. The taxonomic names introduced by Brongniart (1822a, b) were effectively published, in a recognised journal (Mémoires du Museum d'Histoire Naturelle, Paris) and as a separate offprint. Brief diagnoses were given for each genus and section, and although it is not a requirement in a publication this early (ICN, Art. 40.1) a type was indicated (see ICN, Art. 40.3) either by him illustrating a specimen (to which a species names was assigned) or by referring to an illustration and name published in an earlier work, mainly by Schlotheim (1820) or Sternberg (1820). The protologues of many of the

species names that he introduced were not accompanied by a diagnosis (some such as *Sagenaria ophiurus* Brongniart included a close-up of part of the specimen but this does not include sufficient detail to merit being regarded as an "illustration with analysis" under ICN, Art. 38.7). However, as each genus mostly only included one species and there was a diagnosis for that genus, following ICN, Art. 38.5 the generic diagnosis may also be taken as having validated the species name. So, if we follow the regulations laid down in the ICN, where do Brongniart's "genres artificiels" stand now?

Date of publication of the "Classification" paper

The date of publication of the "Classification" is given as May 1822 in Appendix IIIA of the ICN. However, Doweld (2017a) has suggested that there is a complication with the exact dates of publication. Brongniart had read his paper to the Académie des Sciences (Paris) in January 1822 (reported by Richards 1822) and it was then published in the Mémoires du Museum d'Histoire naturelle Paris, the first part between 25th May and 1st June 1822, and the second part between 21st and 28th September 1822 (referred to here as Brongniart 1822a and 1822c, respectively). In addition, there was an offprint which included both parts and this was published on the 24th June 1822 (referred to here as Brongniart 1822b). Consequently, the second part of the paper was published first in the offprint and not in the journal.

Since writing the first draft of this paper, it has been brought to our notice that in the report of Brongniart's oral presentation of his "Classification" paper to the Académie des Sciences (Paris), Achille Richard (1822) quoted Brongniart's generic names and associated them with diagnoses. As Richard's report is dated as February 1822 it pre-dates the publication of Brongniart's (1822a) original paper by about three months. This was not merely an abstract by Brongniart (as suggested by Stafleu and Mennega 1995: 112) but clearly a report by Richard of Brongniart's presentation: it is written in the third person singular whereas Brongniart's published paper is mostly in the first person singular (just occasionally in the first person plural). The generic diagnoses given by Richard are often similar to those published later by Brongniart (1822a), but there are some differences not only in details of the wording: there are in some cases differences in the diagnostic characters referred to, in particular for *Sigillaria* and *Sagenaria* (features of stem articulation and ribbing) and *Stigmaria* (form of the root scars). It is likely that Richard had available a copy of text on which Brongniart (1822a) later based his published classification, but whether Richard was misquoting from this or Brongniart changed his mind as to how the genera should be diagnosed is unclear.

Although Richard's report did not include any species names or any comparative analysis of the genera, for a work this early giving the generic names and diagnoses alone is sufficient to validate publication of those names. As pointed out in the International Fossil Plant Names Index, a strict adherence to the nomenclatural rules would mean that these genera should be attributed to Brongniart in Richard 1822, rather than as is normally done to Brongniart 1822a. However, this would not only change the way these names have been referenced for most of the last nearly 200 years, it introduces some taxonomic ambiguity because of the differences in the generic diagnoses. Moreover, at least two separate works would now have to be referenced, one for the generic names and diagnoses, and another for the type species and discussions on the genera. In an attempt to simplify matters, we have therefore proposed Richard's (1822) paper be supressed, thereby allowing the Brongniart (1822a) paper to stand as the publication of the protologues of these generic names (Cleal and Thomas 2018). The following analysis is based on the assumption that this will be accepted.

Stafleu and Mennega (1995: 112) also mentioned a second, near contemporaneous "abstract" of Brongniart's work, this time in the German language by Froriep (1822: 289). However, this publication is clearly dated as June 1822 and so postdates Brongniart (1822a) with the generic prologues with which we are dealing here.

There is another work published in that year, which also described some of the same species that he dealt with in the "Classification" (by Brongniart 1822d). However, Doweld (in the International Fossil Plant Names Index, http://fossilplants.info/) states that this was published in August of that year and so post-dates Brongniart (1822a, b). Some of the figures and species names included in Brongniart (1822a–c) were also reproduced in Cuvier (1822). This has been reported as being published on the 20th May 1822 (Doweld in the International Fossil Plant Names Index) which would therefore probably pre-date Brongniart (1822a). However, none of the taxonomic names are accompanied by a diagnosis and so were not validly published in Cuvier's (1822) work.

Nomenclature

Brongniart (1822a, b) described 19 genera of plant fossils that he could not place confidently in living taxa. Of these, one genus (*Filicites*) was subdivided into five sections or subgenera but (following Sternberg 1825), Brongniart (1828a) later raised them in rank to genera and this is how they are normally used today. The following analysis will deal with all 24 genera / sections included in the 1822a, b work, including for completeness the two that had been validly published previously by Sternberg (1820). The taxa are dealt with in the same sequence as was given in the table on Brongniart (1822a: 209). In all cases, the diagnoses are as given by Brongniart (1822a, b). For the first part of the paper, pagination is as in the journal rather than the separate offprint, as the former was published first (to calculate the pagination in the offprint, simply subtract 200 from the pagination quoted here); the plate numbers are the same in both. For the second chapter, pagination is as in the offprint, as this predates its appearance in the "Mémoire" (for this, the "Mémoire" pagination can be calculated by adding 258 to the pagination quoted here). Where known, the origin and current location of the nomenclatural types are given; those in the Muséum national d'Histoire naturelle, Paris (MNHN) have been checked against their on-line database, those in the

Národní muzeum, Prague (NM) have been checked against the published catalogue of the Sternberg Collection (Kvaček and Straková 1997). If no data are given, the origin and / or location of the specimen are now unknown. Only homotypic synonymies are listed, although taxonomic synonymies may be mentioned in the discussions of each name.

Brongniart (1822a) adopted some of the generic names used previously by Schlotheim (1820): *Filicites*, *Poacites*, *Palmacites*, *Carpolithes*, *Antholithes*. However, these genera were not validly published in Schlotheim (1820) as he provided no diagnoses (ICN, Art. 38.1); the book moreover pre-dated the starting point for palaeobotanical taxonomy (ICN, Art. 13.1). Schlotheim's names will be referred to but not discussed further.

Nomenclatural acts are being registered in the Plant Fossil Names Registry (PFNR), which is hosted and operated by the National Museum, Prague for the International Organisation of Palaeobotany (IOP), each with a unique registry number.

Systematic palaeobotany

Exogenites Brongniart

1822a *Exogenites* Brongniart, p. 209.

Type. Not designated.

Diagnosis. "Bois formé de couches concentriques régulières."

Discussion. Brongniart (1822b: 41) assigned a number of examples of fossil wood to *Exogenites* (most of which he regarded as dicotyledonous), but none were described or illustrated, nor given a species epithet. In the absence of a designated type or figured specimen, and being based on such a generalised diagnosis, this name is regarded as unusable (Edwards 1931: 40).

Endogenites Brongniart

Text-fig. 1a

1822a *Endogenites* Brongniart, p. 209.

Type. *Endogenites echinatus* Brongniart, 1822b, p. 43, pl. 5, fig. 2; Loc.: Eocene lignite, Vailly, near Soissons, France.(Designated by Andrews 1955: 82).

Diagnosis. "Bois composé de faisceaux de vaisseaux isolés plus nombreux à la circonférence qu'au centre."

Discussion. Brongniart (1822a) created this genus for stems with endogenous growth such as found in palms. According to Farr et al. (1979: 614) no type was designated, but two species were briefly described and so may be regarded as syntypes. *Endogenite* (sic!) *bacillaire* Brongniart (1822a: 211) was based on specimens from two different localities, none of which were figured, and whose current whereabouts are unknown (they are not listed on the MNHN on-line database). We therefore accept the proposal of Andrews (1955) that the other species *Endogenites echinatus* should be taken as the type. Jongmans (1960: 1173) claimed that the name *E. echinatus* had been used earlier by Brongniart (in Cuvier 1811) but this was in error; Brongniart would have been only 10 years old at the time. It was in a later Cuvier publication that Brongniart (1822d: 356) had used the name and, as pointed out earlier, this post-dates Brongniart (1822a).

Brongniart (1828a: 120) later transferred the type to *Palmacites* Brongniart, 1822a, on the assumption that it represented remains of a palm stem. It was later interpreted as a cycad stem and illegitimately renamed *Zamites brongniartii* C.Presl in Sternberg (1838). Until the type has been located and its affinities established, it will be difficult to diagnose a fossil-genus to which this name could be applied, except perhaps for a generalised group of stem fossils with numerous protruding leaf bases, as is shown in the type. However, there has been no suggestion in recent years that such a genus would be useful.

Culmites Brongniart

Text-fig. 1b

1822a *Culmites* Brongniart, p. 209.

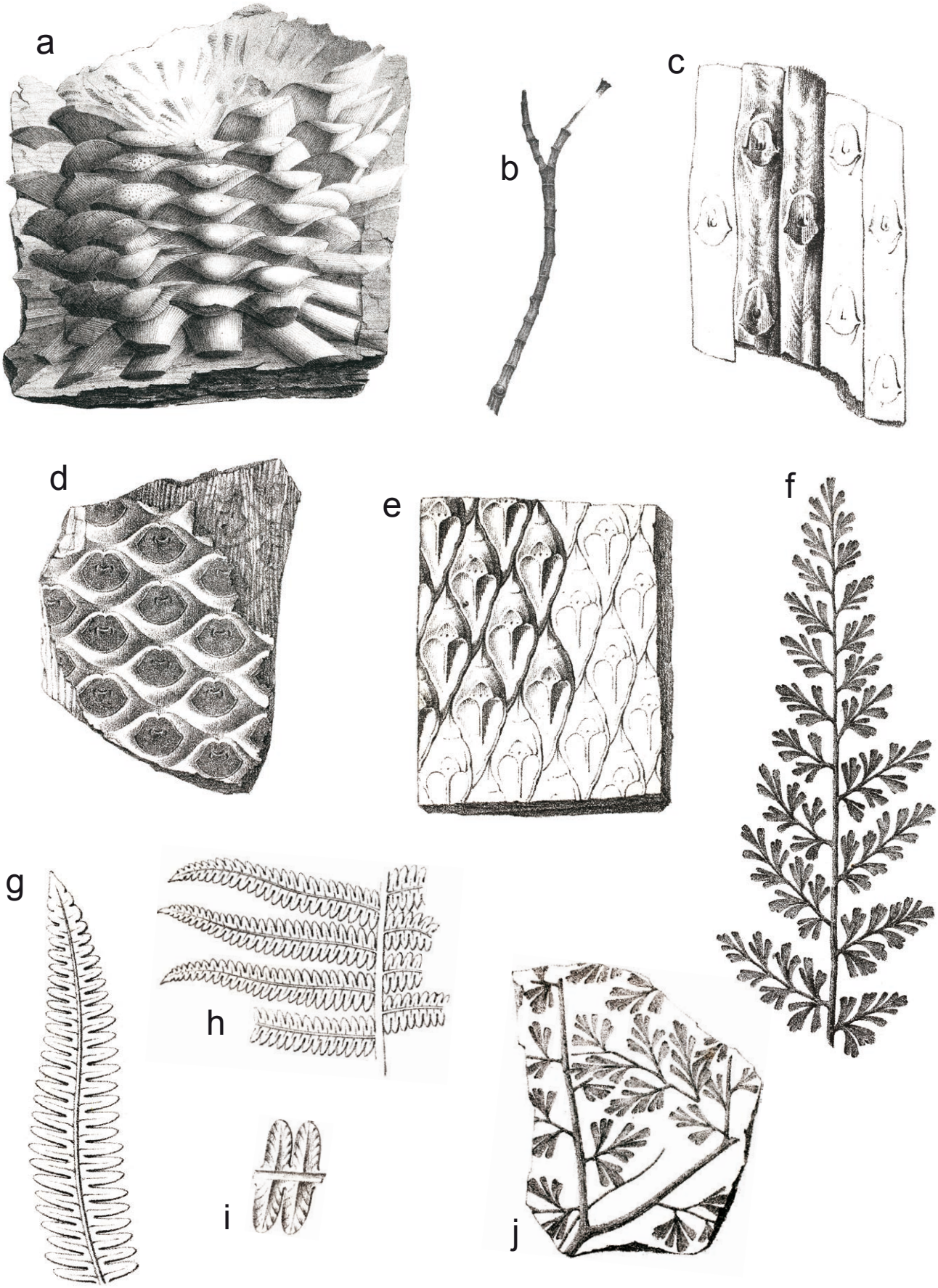
Type. *Culmites nodosus* Brongniart, 1822a, p. 215, pl. 1, fig. 1 (see comments by La Motte 1950: 138); Loc.: Eocene Series, Montrouge near Paris, France. Figured without name by Cuvier (1811: pl. 2, fig. 1F).

Diagnosis. "Tiges articulées lisses, impression unique à chaque articulation."

Discussion. Brongniart (1822a) referred to just one species in the protologue, *Culmites nodosus*. In the later published part of the paper (Brongniart 1822b, c) he established two further species: *Culmites ambiguus* Brongniart, 1822b, p. 45 (Type: Cuvier 1811: pl. 2, fig. 6); and *Culmites anomalus* Brongniart, 1822b, p. 45 (Type: Alexander Brongniart 1810: pl. 23, fig. 15). However, Brongniart (1822b: 45) unequivocally stated that *C. nodosus* is the type.

Brongniart (1822a) compared the type of *Culmites* with stems of various monocots, including grasses, palms and canes. Unger (1850) combined *Culmites* with *Caulinites* Brongniart, 1828a, another fossil-genus used for monocot stems and rhizomes, but later (Unger 1852) separated them again, with no clear explanation given in either case. Until the status of the type of *Culmites* is established, it is difficult to see what role the generic name can have in palaeobotanical taxonomy.

Text-fig. 1. Illustrations from Brongniart (1822a, b) of specimens that remain legitimate taxonomic types of fossil-species. All same scale as in original plate unless otherwise stated. a) *Endongenites echinatus* Brongniart, Eocene lignite, Vailly, near Soissons, France, × 0.5. b) *Culmites nodosus* Brongniart, Eocene Series, Montrouge near Paris, × 0.5. c) *Sigillaria scutellata* Brongniart, MNHN.F.1072.1, unknown locality. d) *Clathraria brardii* Brongniart (≡ *Sigillaria brardii* (Brongniart) Brongniart), Pennsylvanian Subsystem. e) *Sagenaria coelata* Brongniart (≡ *Lepidodendron coelatum* (Brongniart) Brongniart; = *Lepidodendron aculeatum* Sternberg), Pennsylvanian Subsystem. f, j) *Filicites* (*Sphenopteris*) *elegans* Brongniart (≡ *Sphenopteris elegans* (Brongniart) Sternberg), Wadenburg Formation (Serpukhovian Stage), Upper Silesia. g–i) *Filicites* (*Pecopteris*) *penniformis* Brongniart (≡ *Pecopteris penniformis* (Brongniart) Brongniart), Pennsylvanian Subsystem.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Calamites Sternberg typ. et orth. cons.

1820 *Calamites* Schlotheim, p. 398 (nom. inval.).
1820 *Calamitis* Sternberg, p. 24.
1822a *Calamites* Brongniart, p. 209 (orth. cons.).

Type. *Calamites suckowii* Brongniart, 1828b, p. 124 (typ. cons.); Loc.: Middle Pennsylvanian Series, Dudweiler, near Saarbrücken, Germany (see comments in Cleal et al. 2012).

Diagnosis. "Tiges articulées striées régulièrement, impressions arrondies, petites, nombreuses, formant un anneau autour de chaque articulation, ou quelquesfois nulles."

Discussion. The nomenclatural status of *Calamites* has been the subject of some confusion and a number of proposals have been made (Lanjou 1953, Anon. 1954, Storch 1981, Greuter et al. 1994, Cleal et al. 2012). The position summarised above is that given in the most recent proposal (Cleal et al. 2012) and is the basis for its status as a conserved name in the current ICN.

The name is widely used for a fossil-genus of adpressions, casts and pith-casts of stems and rhizomes, mainly from Carboniferous and Permian floras, and usually regarded as belonging to the Sphenophyta (e.g. Jongmans 1911, Crookall 1969). Their anatomy is well documented (e.g. Andrews 1952, Eggert 1962, Rössler and Noll 2006, 2007) and there are three basic structural types that are generically distinguished: *Calamitea* Cotta, 1832, *Arthropitys* Goeppert, 1864, and *Arthroxylon* Reed, 1952. Since it is impossible to determine which of these anatomies corresponds to the nomenclatural type of *Calamites*, the latter should only be used for adpressions, casts and pith-casts, and not for anatomically-preserved fossils.

Syringodendron Sternberg

1820 *Syringodendron* Sternberg, p. 24.
1822a *Syringodendron* Brongniart, p. 209.

Type. *Syringodendron organum* Sternberg, 1820, pl. 13, fig. 1; Loc.: Middle Pennsylvanian Series, Žacléř, the Czech Republic (designated by Andrews 1955: 247).

Diagnosis. "Tiges cannelées, non articulées, impressions punctiformis ou linéaires disposes en quinconce."

Discussion. Brongniart (1822a: 209) simply followed Sternberg (1820) in his use of this name. The Sternberg type and the specimen figured by Brongniart (1822a: pl. 1, fig. 3) are both fragments of stem with strongly-developed ribs on which are longitudinal rows of pairs of small scars (parichnos traces). It is widely accepted (e.g. Crookall 1966) that they are stems of *Sigillaria* Brongniart where the outer layer of periderm including the leaf bases has been lost. Crookall (1966: 355) went as far as to synonymise *Syringodendron* and *Sigillaria*, but this would result in *Sigillaria* having to be suppressed in favour of *Syringodendron*; although *Sigillaria* is a conserved name (see below), *Syringodendron* is not one of the names it is specifically conserved against. Since few of the characters that are normally used to classify *Sigillaria* stems are preserved in the decorticated *Syringodendron* stems, combining the two fossil-genera would make little practical sense. Moreover, since the decorticated and non-decorticated stems arguably represent different states of preservation and yield different types of taxonomic information, there is no requirement for them to be synonymised. Therefore, *Syringodendron* should only be used for decorticated stems.

Sigillaria Brongniart nom. cons.
Text-fig. 1c

1821 *Rhytidolepis* Sternberg, p. 32 (nom. rej.).
1822a *Sigillaria* Brongniart, p. 209 (nom. cons., non *Sigillaria* Rafinesque ex Nuttall, 1819).

Type. *Sigillaria scutellata* Brongniart, 1822a, p. 222, pl. 1, fig. 4; MNHN.F.1072.1; Loc.: Middle Pennsylvanian Series, Puits du Moulin, Anzin, Département du Nord, France (vide Brongniart 1837b: 455).

Diagnosis. "Tiges cannelées, non articululées, impressions en forme de disques disposées en quinconce."

Discussion. This name is widely used for Palaeozoic lycopsid stems with the spirally formed leaf scars or cushions secondarily arranged in longitudinal rows. Sternberg (1820) placed them within "*Lepidodendron* Sternberg tribe *Alveolariae* Sternberg", but were later assigned to a separate genus *Sigillaria* by Brongniart (1822a); although published earlier, *Alveolariae* does not take precedence over *Sigillaria* as it is invalid, having been designated as a tribe rather than a taxon at a sub-generic rank (ICN, Art. 37.6). *Sigillaria* has been conserved since the Vienna ICBN (McNeill et al. 2006; see Zijlstra 2001 for details of the proposal; also Vogellehner 1968) but only against an earlier homonym *Sigillaria* Rafinesque ex Nuttall, 1819 (a genus of living angiosperms) and a heterotypic synonym *Rhytidolepis* Sternberg, 1821 (the possible conflict with *Syringodendron* Sternberg has been dealt with above).

The type of *Sigillaria* is a stem adpression but Brongniart (1839) later also used the name for an anatomically-preserved fossil (see also ICN, Art. 11.1, Ex. 1). All *Sigillaria*-like petrifactions that have been described (e.g. Lemoigne 1960) have essentially the same anatomy and there seems little justification for assigning them to a different fossil-genus to the casts or adpressions.

Clathraria Brongniart
Text-fig. 1d

1822a *Clathraria* Brongniart, p. 209.

Type. *Clathraria brardii* Brongniart, 1822a, p. 222, pl. 1, fig. 5; Loc.: Upper Pennsylvanian Series, Lardin-Saint-Lazare, near Terrasson, Département de la Dordogne, France (vide Brongniart 1837b: 431); ≡ *Sigillaria brardii* (Brongniart) Brongniart, 1828a.

Diagnosis. "Tiges ni cannelées, non articululées, impressions en forme de disques arrondis disposées en quinconce."

Discussion. This generic name was used by Brongniart (1822a) for stem fossils similar to *Sigillaria* but with no rib between the longitudinal rows of leaf cushions. Most authors now assign both types of stem to *Sigillaria*,

although Crookall (1966) argued that they could be used to distinguish sections within the genus.

Sagenaria Brongniart nom. illegit.

Text-fig. 1e

1820 *Lepidodendron* Sternberg, p. 23 (pars).
1822a *Sagenaria* Brongniart, p. 209 (nom. illegit.).

Type. Designated here. *Lepidodendron aculeatum* Sternberg, 1820, p. 23, pl. 6, fig. 2; pl. 8, fig. 1; Loc.: Radnice Member (upper Bashkirian Stage), Radnice, the Czech Republic; photographically refigured by Kvaček and Straková (1997: pl. 2, fig. 1).

Plant Fossil Names Registry Number. PFN000143 (for type designation).

Diagnosis. "Tiges sans articulations ni cannelures, couvertes de tubercles rhomboïdaux, coniques, disposes en quinconce, pourtant à leur sommet une impression en forme disque."

Discussion. Brongniart (1822a) used this generic name for *Lepidodendron* sect. *Lepidotae* Sternberg, 1820 (Sternberg 1820 had illegitimately referred to these sections as "tribes"). Brongniart (1822a) also included two new species within the genus: "*Sagenaria coelata*" Brongniart, 1822a and "*Sagenaria ophiurus*" Brongniart, 1822a. However, these latter two names were probably not validly published here as they were unaccompanied by diagnoses; an illustration with a close-up of the shoot was given for *S. coelata* but this does not show the diagnostic characters sufficiently to count as an "illustration with analysis" to validate the species epithet under ICN, Art. 38.7–9. The only previous proposal to typify *Sagenaria* was by Andrews (1955) with "*S. coelata*" but this has to be rejected as that species was not validly published in 1822. A lectotype for *Sagenaria* must therefore be selected from the species listed by Sternberg (1820) under *Lepidodendron* sect. *Lepidotae*, as Brongniart was clearly (albeit indirectly) including them within the genus (ICN, Arts 10.2, 10.3). In order to simplify the situation, we designate here *Lepidodendron aculeatum* Sternberg, 1820 as lectotype of *Sagenaria* – it is conspecific with one of the specimens illustrated by Brongniart (1822a: pl. 12, fig, 6 – as "*S. coelata*").

The genus *Lepidodendron* was originally based on external morphological characters of the stem as seen in adpressions and casts. However, subsequent work on coal ball specimens has resulted in the stems being subdivided into a number of other fossil-genera based on anatomical features, including *Diaphorodendron* DiMichele, 1985, *Synchysidendron* DiMichele et Bateman, 1992, and *Hizemodendron* Bateman et DiMichele, 1991. A fourth fossil-genus was recognised on anatomical characteristics in coal ball fossils, based round the species *Lepidodendron hickii* Watson, 1907. DiMichele (1983) stated that *L. hickii* has deep ligule pits and infrafoliar parichnos, with the larger cushions having a relatively broad lower surface and a low keel with plications, and is very similar to the leaf cushions of the type species of *Lepidodendron* (the adpression species *L. aculeatum*). Bateman and DiMichele (1991: 195) went further and stated that *L. hickii* is the anatomically preserved equivalent of *L. aculeatum*, and as a consequence, *L. hickii* would have to be regarded as a later heterotypic synonym of *L. aculeatum* and so supressed.

This more refined generic classification undoubtedly provides a better systematic resolution of the anatomically preserved fossils but there are problems when trying to use it with the more commonly found adpressions and casts of the stems. One of the characters used for distinguishing these fossil-genera (the presence or absence of infrafoliar parichnos) can sometimes be recognised in adpressions and casts, but relying entirely on just this one feature as a diagnostic feature may give a false impression of certainty with such fossils and make comparisons much more difficult (Laveine et al. 2003). In our view, a better solution is to have separate taxonomies for the adpressions / casts and for the anatomically preserved fossils. Since the type of *Lepidodendron* is an adpression, that name should only be used for such fossils, and an alternative generic name is needed for the group of anatomically-preserved species centred on "*Lepidodendron*" *hickii*.

Stigmaria Brongniart

1820 *Variolaria* Sternberg, p. 22 (nom. illegit., non *Variolaria* Persoon, 1795).
1822a *Stigmaria* Brongniart, p. 209.

Type. *Variolaria ficoides* Sternberg, 1820, p. 24, pl. 12, fig. 1–3 (vide Kvaček and Straková 1997); preserved syntype NM-E 80; Loc.: Radnice Member (upper Bashkirian Stage), Radnice, the Czech Republic; photographically refigured by Kvaček and Straková (1997: pl. 18, fig. 5); ≡ *Stigmaria ficoides* (Sternberg) Brongniart, 1822a.

Diagnosis. "Tiges sans articulations ni cannelures, impressions arrondies, espacées, disposées en quinconce."

Discussion. Brongniart rejected Sternberg's earlier published name of *Variolaria* for this fossil-genus because it was pre-occupied by the name of a lichen genus, *Variolaria* Persoon, 1795. As Brongniart clearly regarded *Stigmaria* as a replacement name for *Variolaria* Sternberg and not a new genus, the type of the former must be taken as the type of the latter, not the specimen figured by Brongniart (1822a: pl. 1, fig. 7).

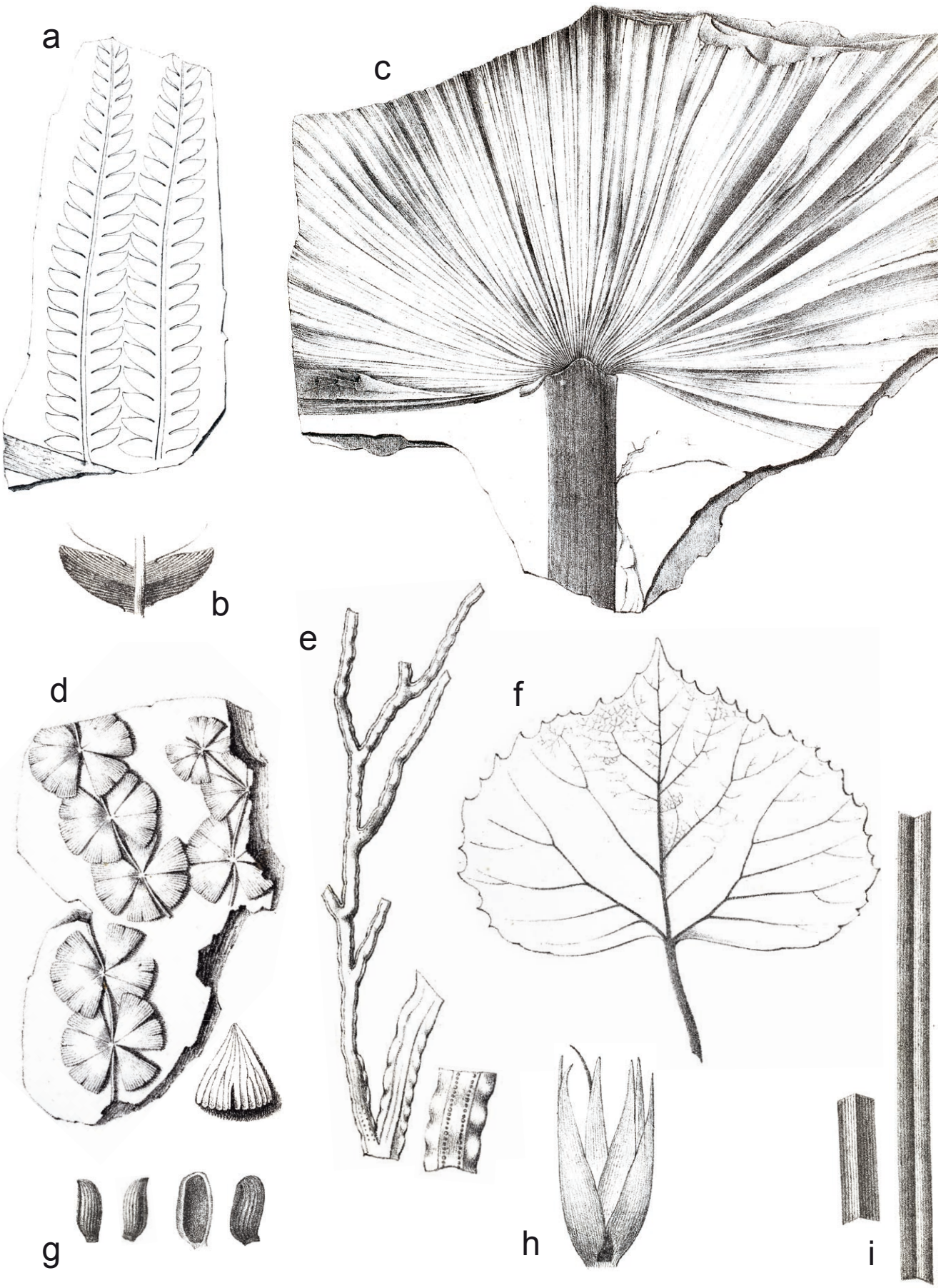
Stigmaria is now used for the rhizomorphs of various arborescent lycopsids with upright stems assignable to fossil-genera such as *Lepidodendron* Sternberg, *Lepidophloios* Sternberg, 1825 and *Sigillaria* Brongniart. The *Stigmaria* rhizomorphs that were attached to these different types of upright stems are indistinguishable morphologically and anatomically, and so it is impossible to assign them to a particular type of stem. *Stigmaria* should, therefore, be retained for these fossil rhizomorphs in all modes of preservation (see Thomas and Seyfullah 2015).

Lycopodites Brongniart nom. rej.

Text-fig. 3a

1820 *Lycopodiolithes* Schlotheim, p. 412 (nom. inval.).
1822a *Lycopodites* Brongniart, p. 209 (nom. rej. vide Pal and Gosh 1990).

Type. *Lycopodites taxiformis* Schlotheim ex Brongniart, 1822a, p. 231, pl. 2, fig. 1.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Diagnosis. "Feuilles linéaires ou setacées sans nervures, ou transverses par une seule nervure insérées tout autour de la tige ou sur deux rangs."

Discussion. Brongniart (1822a) used the name for various types of leafy shoot with small, simple leaves (now referred to microphylls) and grouped them into three informal sections: (1) shoots that were probably attached to arborescent lycopsid stems he called *Sagenaria* (= *Lepidodendron*); (2) shoots that are similar to *Lycopodites taxiformis* with stiff leaves in two rows, and which today are widely regarded as Palaeozoic conifer shoots (e.g. Florin 1938-1945); and (3) shoots that he regarded as possibly the remains of herbaceous lycopsids, such as the Cenozoic *Lycopodites squamatus* Brongniart, 1822a (although others have interpreted this species as a bryophyte or conifer – Unger 1850, Seward 1910). Most subsequent authors have adopted the name for shoots of herbaceous lycopsids. However, in the generic protologue Brongniart (1822a) clearly stated that he regarded the second section, now know to comprise conifer remains, to be most typical ("c'est ce groupe que nous pensons qu'on doit réserver particulièrement ce nom de *Lycopodites*") and so *L. taxiformis* must be taken as the generic type (Pal and Gosh 1990). To allow the continued widespread use of the generic name for lycopsid shoots to continue, *Lycopodites* Lindley et Hutton, 1833, has, therefore, been conserved over *Lycopodites* Brongniart (based on a proposal by Pal and Gosh 1990) since the St Louis ICBN (Greuter et al. 2000).

Filicites Schlotheim ex Brongniart nom. utique rej.

1820 *Filicites* Schlotheim, p. 403. (nom. inval.).
1822a *Filicites* Brongniart, p. 209 (nom. utique rej.).

Type. *Filicites* (sect. *Pecopteris*) *penniformis* Brongniart, 1822a, p. 233, pl. 2, fig. 3 (original spelling "*pennæformis*" – see ICN, Art. 60.8); type designated by Doweld (2012); Loc.: Middle Pennsylvanian Series, Dudweiler, near Saarbrücken, Germany (vide Brongniart 1836: 345).

Diagnosis. "Fronde dispose dans un même plan, symétrique, nervures secondaires simples, dichotomes ou rarement anastomosées."

Discussion. Following Schlotheim (1820), Brongniart (1822a) used this name for all fern-like fronds that could not be attributed to a living genus. Brongniart divided it into a series of sections or subgenera based mainly on pinnule shape and venation, which Sternberg (1825) subsequently raised in rank to genera (accepted by Brongniart 1828a); it is as fossil-genera that they are normally used today. However, *Filicites* remained a legitimate name and had the potential to interfere with the currently accepted nomenclature. Doweld (2012) designated the holotype of *Filicites* (sect. *Pecopteris*) *penniformis* as the type of *Filicites* and then proposed that the generic name *Pecopteris* should be conserved over *Filicites*. Cleal (2012) instead proposed the simpler solution that *Filicites* should be supressed: this was supported by the IAPT Fossil Plant Committee and eventually accepted by the 2017 International Botanical Congress at Shenzen.

Filicites sect. *Glossopteris* Brongniart
Text-fig. 3b

1822a *Filicites* (*Glossopteris*) Brongniart, p. 232.
1825 *Glossopteris* (Brongniart) Sternberg, Tentamen p. xv (nom. rej.).

Type. *Filicites* (sect. *Glossopteris*) *dubius* Brongniart, 1822a, p. 232, pl. 2, fig. 4; Loc.: Pennsylvanian Subsystem; ≡ *Glossopteris dubius* (Brongniart) Sternberg, 1825, Tentamen p. xv).

Diagnosis. "fronde simple, entire, transversée par une seul nervure médiane sans nervures secondaires distinctes."

Discussion. The type of *Filicites* (*Glossopteris*) was later re-interpreted by Brongniart (1828a: 87) as a leaf (now regarded as a cone sporophyll) of an arborescent lycopsid, and as a result used the name *Glossopteris* for a completely different type of leaf with often anastomosing lateral veins. Brongniart's (1828a) use of the name is widely accepted today (e.g. Chandra and Surange 1979) and to avoid it being supressed in favour of the earlier (1822a) homonym (also of the even earlier homonym *Glossopteris* Rafinesque, 1815) the former has been listed as a conserved name with a conserved type since the Paris ICBN (Stafleu 1957).

Filicites sect. *Sphenopteris* Brongniart
Text-fig. 1f, j

1822a *Filicites* (*Sphenopteris*) Brongniart, p. 233.
1825 "*Sphaenopteris*" (Brongniart) Sternberg, Tentamen p. xv.

Type. *Filicites* (sect. *Sphenopteris*) *elegans* Brongniart, 1822a, p. 233, pl. 2, fig. 2; Loc.: Waldenburg Formation (Serpukhovian Stage), Upper Silesia; ≡ "*Sphaenopteris*" *elegans* (Brongniart) Sternberg, 1825, Tentamen p. xv.

Diagnosis. "pinnules cunéiformes, arrondies ou lobées à l'extrémié, et les nervures palmées ou rayonnantes de la base de la pinnule."

Discussion. It is incorrectly stated in the International Fossil Plant Names Index (http://fossilplants.info/) that the first use of *Sphenopteris* as a genus is in Sternberg (1823: 36), but Sternberg clearly stated that he regarded it here as a section ("Abteilung") and earlier (p. 27) that it was of

Text-fig. 2. Illustrations from Brongniart (1822a, b) of specimens that remain legitimate taxonomic types of fossil-species. All same scale as in original plate unless otherwise stated. a, b) *Filicites* (*Odontopteris*) *brardii* Brongniart (≡ *Odontopteris brardii* (Brongniart) Sternberg) (a × 0.5). c) *Palmacites lamanonis* Brongniart, Miocene Series, Aix-en-Provence, France, × 0.67. d) *Sphenophyllites emarginatus* Brongniart (≡ *Sphenophyllum emarginatum* (Brongniart) Brongniart). e) *Fucoides strictus* Agardh ex Brongniart, L'ile de Aix lignite mine, near La Rochelle, France. f) *Phyllites populina* Brongniart (≡ *Populus populina* (Brongniart) Knobloch), Miocene Lagerstätte, Öhningen, Switzerland. g) *Carpolithes thalictroides* Brongniart (≡ *Stratiotes thalictroides* (Brongniart) Chandler), upper Oligocene Calcaire de Beauce, Paris Basin, France. h) *Antholithes liliacea* Brongniart, Eocene Monte Bolca Lagerstätte in Veneto, Italy. i) *Poacites carinata* Brongniart, Pennsylvanian Subsystem.

Filicites. The first use of *Sph(a)enopteris* as a generic name is in the 1825 Tentamen of Sternberg. Although when first used as a generic name the spelling was altered to *Sphaenopteris* by Sternberg (1825), the original orthography of Brongniart's (1822a) section must be retained (ICN, Art. 60.1).

This is one of the most confused of the Brongniart fossil-taxa, and is still regularly used for both fern and seed-plant fossil-species. However, the type (*S. elegans*) is well-documented as a Mississippian-age early seed-plant (e.g. Kidston 1923-1925: 242) and so the name *Sphenopteris* should only be applied to this group of early seed-plant fronds. It should be noted in passing that Kidston adopted for this species the taxonomic synonym *Diplotmema adiantioides* (Schlotheim ex Potonié) Gothan, 1913 (≡ *Cuneatopteris adiantoides* Schlotheim ex Potonié, 1907, p. 2) since the first use of the species epithet (as "*Filicites adiantoides*" Schlotheim, 1820) pre-dated both Brongniart's and Sternberg's works. However, as "*F. adiantioides*" was published prior to the starting point for publication of fossil-taxa (ICN, Art. 13.1) this must be rejected.

This raises a practical problem with classifying some fossil fern fronds with small lobed pinnules, especially of Palaeozoic age. Although there are numerous well-defined fossil-genera for such ferns (e.g. *Renaultia* Zeiller, 1883, *Zeilleria* Kidston, 1884) these are diagnosed by their reproductive structures. Those species for which reproductive structures are unknown have tended to be placed in *Sphenopteris* (e.g. Brousmiche 1983) but this is not tenable given that the type of that name is a seed-plant. There is in fact no available legitimate name for a fossil-genus of species of such fern fossils for which reproductive structures are unknown. It would be possible to establish an "artificial" genus for such species; this would be analogous to the fossil-genus *Taeniopteris* Brongniart, 1828a nom. cons., which is now used for entire cycadophyte-like leaves for which neither cuticles nor reproductive structures are known (van Konijnenburg-van Cittert et al. 2017). However, to date no such fossil-genus has been established for these fern fossils. Another option would be to revert to Brongniart's (1822a) original conception for *Sphenopteris* as including all pteridophyllous foliage with lobed pinnules and supressing names such as *Renaultia* and *Zeilleria* but this would seem a retrograde step. The only viable option within the current framework of the ICN is to make a judgement as to the taxonomic position of such species based on similarities in the morphology of the sterile foliage, maybe using an open-nomenclature-like qualifier similar to that used in palaeozoology (Matthews 1973, Bengtson 1988).

In passing, mention should be made of a later homonym of *S. elegans*, *Sphenopteris elegans* (Yokoyama) Ôisi, 1940 (≡ *Onychiopsis elegans* Yokoyama, 1895) based on a type from the Lower Cretaceous Series of Japan.

Filicites sect. *Nevropteris* Brongniart

Text-fig. 3d

1822a *Filicites* (*Nevropteris*) Brongniart, p. 233.
1825 *Neuropteris* (Brongniart) Sternberg, Tentamen p. xi (nom. rej.).

Type. *Filicites* (sect. *Nevropteris*) *heterophyllus* Brongniart, 1822a, p. 233, pl. 2, fig. 6; Loc. Middle Pennsylvanian Series, Saarbrücken, Germany (vide Brongniart 1831a: 243).

Diagnosis. "pinnules arrondies, non adherents au rachis, par leur base; les nervures s'épanuoissent du point d'insertion de la pinnule, et sont en general très-distinctes et dichotomes."

Discussion. The problems surrounding the type of this name have been discussed by Laveine and Blanc (1996) and Laveine (1998) with the result that since the St Louis ICBN (Greuter et al. 2000) it has been conserved with the specimen figured by Brongniart (1831: pl. 71) as type rather than that figured in the protologue of the basionym. The spelling used by Sternberg (1825) was also conserved against that used by Brongniart (1822a).

The name is now mostly used for Palaeozoic medullosalean foliage (Cycadopsida) with basally constricted pinnules and non-anastomosed veining. Such fossils have been extensively recorded and studied, with the result that Brongniart's original fossil-genus has now been segregated into a series of more tightly circumscribed genera based initially on frond architecture (Gothan 1941) and then later incorporating data on epidermal anatomy (Cleal et al. 1990, Cleal and Shute 1995). As pointed out by Cleal and Shute (1995) there remain a few species that are morphologically well circumscribed but for which frond architecture or cuticles are insufficiently known for them to be placed in this more refined classification. These tend to be retained within *Neuropteris* but with no implication being made that they are related to the type of that fossil-genus (*N. heterophylla*).

The name is usually used for adpression fossils, although it can also be used for anatomically-preserved fossils if sufficient morphological characters are available, such as from paradermal sections (e.g. Beeler 1983). However, if only anatomical data are available, *Neuropteris* is difficult to distinguish from other types of medullosalean frond (e.g. *Alethopteris* Sternberg, 1825) and so the more widely circumscribed fossil-genus defined exclusively on anatomical characters (*Myeloxylon* Brongniart, 1849) is best used.

Filicites sect. *Pecopteris* Brongniart

Text-fig. 1g–i

1822a *Filicites* (*Pecopteris*) Brongniart, p. 233.
1825 *Pecopteris* (Brongniart) Sternberg, Tentamen p. xvii.

Type. *Filicites* (sect. *Pecopteris*) *penniformis* Brongniart, 1822a, p. 233, pl. 2, fig. 3; Loc. Middle Pennsylvanian Series, Dudweiler, near Saarbrücken, Germany (vide Brongniart 1836: 345); ≡ *Pecopteris penniformis* (Brongniart) Brongniart, 1828a.

Diagnosis. "la fronde est pinnatifide à pinnules adherents par leur base au rachis, transversée par une nervure médiane et à nervures secondaires pennées."

Discussion. When Sternberg (1825) raised this species in rank to genus, he illegitimately renamed the type species *Pecopteris pennata* Sternberg, 1825, but this name must be supressed as a later homotypic synonym. In the original definition of Brongniart (1822a) this name was used for both fern and seed-plant fronds. However, mainly

through the separation off of species with larger pinnules such as *Alethopteris* Sternberg, 1825, and *Callipteridium* (E. Weiss) Grand'Eury, 1877 (≡ *Odontopteris* (*Callipteridium*) E.Weiss, 1870) the name has become almost exclusively used for Palaeozoic fern foliage. Only fronds of the seed-plant family Callistophytaceae Stidd et Hall, 1970, have occasionally still been referred to *Pecopteris*, but even this is nowadays unusual; such fronds are normally now referred to *Dicksonites* Sterzel, 1881.

Most Palaeozoic pecopteroid foliage belong to two families: the Psaroniaceae Unger ex Endlicher, 1842, (Marattiales) and Tedeleaceae Eggert et Taylor, 1966, (Botryopteridales). The type of *Pecopteris* unequivocally belongs to the family today usually referred to as the Tedeleaceae and so the name should be restricted to species belonging to that family, most notably *P. penniformis*, *Pecopteris plumosa* (Artis) Brongniart, 1836 (≡ *Filicites plumosus* Artis, 1825) and *Pecopteris volkmannii* Sauveur, 1848. These species have in the past been placed in a separate fossil-genus based on the distinctive soral structures, variously named *Senftenbergia* Corda, 1845 and *Dactylotheca* Zeiller, 1883, but (as pointed out by Cleal 2015) these names should be supressed as later taxonomic synonyms of *Pecopteris*.

On this basis, *Pecopteris* should not be used for species that are demonstrably attributable to the Psaroniaceae. Most of the well-established Psaroniaceae fossil-species can be assigned to one or other of the fossil-genera that are based on a combination of pinnule morphology and venation, and sporangial form (as summarised in Cleal 2015).

Filicites sect. *Odontopteris* Brongniart

Text-fig. 2a, b

1822a *Filicites* (*Odontopteris*) Brongniart, p. 234.
1825 *Odontopteris* (Brongniart) Sternberg, Tentamen p. xxi (nom. cons.).

Type. *Filicites* (sect. *Odontopteris*) *brardii* Brongniart, 1822a, p. 234, pl. 2, fig. 5; Loc. Upper Pennsylvanian Series, Lardin-Saint-Lazare, near Terrasson, Département de la Dordogne, France (vide Brongniart 1831b: 252); ≡ *Odontopteris brardii* (Brongniart) Sternberg, 1825, Tentamen p. xxi (original spelling "*Berardi*").

Diagnosis. "plantes dont les pinnules sont adherents au rachis par toute leur base sans nervure médiane, et dont les nervures secondaires partent toutes perpendiculairement de ce rachis."

Discussion. This use of the name *Odontopteris* has been conserved against an earlier homonym that had been based on an extant fern (*Odontopteris* Bernhardi, 1801 – see Cleal and Shute 1991). Otherwise, the nomenclature is straightforward with the name being mostly used for frond adpressions of Palaeozoic Medullosales with pinnules that are broadly attached to the supporting rachis. There has to date been no unequivocal record of such fronds as anatomically preserved fossils.

Sphenophyllites Brongniart nom. rej.

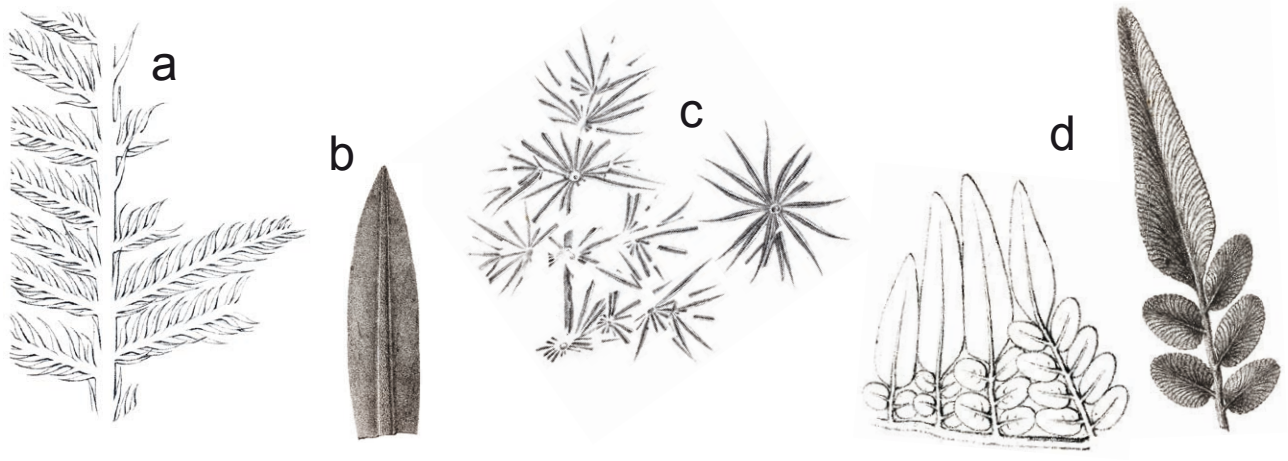
Text-fig. 2d

1822a *Sphenophyllites* Brongniart, p. 209 (nom. rej.).
1821 *Rotularia* Sternberg, p. 33 (nom. rej.).
1828a *Sphenophyllum* Brongniart, p. 68 (nom. cons.).

Type. *Sphenophyllites emarginatus* Brongniart, 1822a, p. 234, pl. 2, fig. 8; ≡ *Sphenophyllum emarginatum* (Brongniart) Brongniart, 1828a, p. 68.

Diagnosis. "Feuilles verticillées, cuneiforms, tronquées, à nervures rayonnantes, dichotomes."

Discussion. The changes in name of this fossil-genus were summarised by Vogellehner (1967), who proposed the conservation of *Sphenophyllum* Brongniart, 1828 over the earlier names, and this has been adopted since the Seattle ICBN (Stafleu et al. 1972). There was an earlier use of the generic epithet *Sphenophyllum*, by König (1825) and this is sometimes quoted for the combination *Sphenophyllum emarginatum* (e.g. Andrews 1955). However, the combination is simply given by König in a



Text-fig. 3. Illustrations of specimens in Brongniart (1822a, b) that were originally generic or section types but which have been subsequently supressed; see text for further details. All reproduced half original size, except d which is original size. a) *Lycopodites taxiformis* Schl. ex Brongniart. b) *Filicites* (*Glossopteris*) *dubius* Brongniart (≡ *Glossopteris dubius* (Brongniart) Sternberg), Pennsylvanian Subsystem. c) *Asterophyllites radiatus* Brongniart (≡ *Annularia radiata* (Brongniart) Sternberg). d) *Filicites* (*Neuropteris*) *heterophylla* Brongniart (≡ *Neuropteris heterophylla* (Brongniart) Sternberg), Pennsylvanian Subsystem, Saar-Lorraine.

plate caption, without accompanying text or even direct reference to Brongniart or his 1822a paper, so is widely regarded as being not validly published (e.g. Zeiller 1888: 708). [König's publication is listed in the "British National Bibliography" (http://bnb.bl.uk/) as published in 1830, but most authors have quoted an 1825 date and there was at least one contemporaneous press review (Taylor 1825) appearing to confirm the earlier publication date.]

The generic type has not been definitely identified but there is some comparison between the figured drawing in Brongniart (1822a: pl. 2, fig. 8) and specimen MNHN.F.3519.1 which is a specimen of *Sphenophyllum emarginatum* from the Saar-Lorraine Coalfield.

The nomenclature of this fossil-genus is otherwise relatively uncomplicated, and can legitimately be used for foliage, both as adpressions and anatomically preserved fossils.

Asterophyllites Brongniart nom. rej.

Text-fig. 3c

1822a *Asterophyllites* Brongniart, p. 210 (nom. rej.).

Type. *Asterophyllites radiatus* Brongniart, 1822a, p. 235, pl. 2, fig. 7; ≡ *Annularia radiata* (Brongniart) Sternberg, 1825, Tentamen p. xxxi.

Diagnosis. "Feuilles verticillées, à une seule nervure."

Discussion. Brongniart (1822a) initially used this generic name for all fossils leaves that have a single vein and are arranged in whorls around the stem. However, Brongniart seems to have been unaware that there was a pre-existing name for an almost identical genus (although with different types) – *Annularia* Sternberg, 1821. In the same work, Sternberg had also created a second genus (*Schlotheimia* Sternberg) for articulated stems with leaf whorls at the nodes.

Sternberg (1825) later confused the issue by dividing *Schlotheimia* into *Bornia* Sternberg, 1825, and *Brukmannia* Sternberg, 1825, the former for leaves he regarded as being from trees, the latter for whorls of more slender, rigid leaves that he regarded as coming from herbaceous plants (he illegitimately abandoned his earlier name *Schlotheimia*). In addition he referred a heterogeneous group of fossil sphenopsids shoots to a genus he named *Bechera* Sternberg, 1825, but Doweld (2017a) has shown this name to be nomenclaturally superfluous (it also included the type of an existing name of the charophyte genus *Gyrogonites* Lamark, 1801). All of these generic distinctions are now rejected as taxonomically unhelpful (e.g. Jongmans 1911).

Brongniart (1828a) later accepted the original view of Sternberg (1821) that two genera could be distinguished for these leaf whorls, adopting the latter's *Annularia*, and illegitimately using his own original name *Asterophyllites* for *Schlotheimia*. This distinction and nomenclature has subsequently been almost universally accepted in the palaeobotanical literature (e.g. Jongmans 1911, Abbott 1958). Unfortunately, however, the original type of *Asterophyllites* was now within the circumscription of *Annularia*. To avoid substantial disruption to palaeobotany (transferring the many *Annularia* species to *Asterophyllites*, and the species usually included within *Asterophyllites* to *Schlotheimia*) Vogellehner (1967) proposed that Brongniart's (1828a) nomenclature for these fossils should be conserved and this was included in the Seattle ICBN (Stafleu et al. 1972).

Fucoides Brongniart (original spelling "*Fucoïdes*")

Text-fig. 2e

1822a *Fucoïdes* Brongniart, p. 210.
1833 *Rhodomelites* Sternberg, p. 25 (nom. illegit.).

Type. *Fucoides strictus* Agardh ex Brongniart, 1822a, p. 237; Loc: L'ile de Aix lignite (Cenomanian Stage), mines near La Rochelle, France.

Diagnosis. "Fronde non symétrique, souvent disposée dans un même plan, à nervures, nulles ou mal limitées."

Discussion. Brongniart (1823) published a detailed analysis of fossil remains he regarded as probably of marine algal origin but few subsequent palaeobotanists have devoted much attention to them. Some of the species included by Brongniart (1823) in *Fucoides* have subsequently been reinterpreted as animal remains (e.g. Maletz 2011) or trace fossils (Jensen and Bergström 1995) and so their names would come outside of the remit of the ICN; but the generic type appears to be of plant (or, at least, algal) origin. Nevertheless, although *Fucoides* is legitimately published, it will be difficult to use the name until the systematic position of the type has been established.

Andrews (1955) in error attributed *Fucoides* to Brongniart (1823) and stated that the (lecto)type was *Fucoides orbignianus* Brongniart, 1823. However, the name had been validly published a year earlier (Brongniart 1822a) with only one species name mentioned (*F. strictus*), which should therefore be taken as the indicated type.

Phyllites Brongniart

Text-fig. 2f

1822a *Phyllites* Brongniart, p. 210.

Type. Designated here. *Populus latior* A.Braun, 1845, p. 169 (figured Heer 1855: pl. 53, fig. 1); Loc.: Miocene Lagerstätte, Öhningen, Switzerland; ≡ *Populus populina* (Brongniart) Knobloch, 1964 nom. illegit. – see Doweld 2017b.

Plant Fossil Names Registry Number. PFN0000147 (for type designation).

Diagnosis. "Feuilles à nervures bien limitées, plusieurs fois divisées ou anastomosées."

Discussion. It has been widely assumed that Brongniart (1822a) only included a single species (*Phyllites populinus* ("*populina*") Brongniart) in this genus (e.g. Kvaček 2008) and that this was therefore the generic type (e.g. Andrews 1955). However, this species name was not validly published by Brongniart (1822a) as no diagnosis was provided and there is only a single outline drawing of a single leaf with partial indication of the venation (Brongniart 1822a: pl. 3, fig. 4); the latter is totally inadequate to be regarded as "an illustration with analysis" that might validate the name through ICN, Art. 38.9 (the ICN Glossary defines

an "analysis" as a "figure or group of figures, commonly separate from the main illustration of the organism … showing details aiding identification"). Moreover, Brongniart (1822a: 238) also mentioned a second species, which he later in the same work described and figured as *Phyllites multinervis* Brongniart (Brongniart 1822b: 51; pl. 5, fig. 4). Brongniart (1822a) regarded this as rather different from *P. populinus*, and later transferred it to another genus as *Potamophyllites multinervis* (Brongniart) Brongniart, 1828a, p. 114. Nevertheless, because two species names were mentioned in Brongniart (1822a) the generic diagnosis alone cannot be used to validate either *P. populinus* or *P. multinervis*. Consequently, as neither species mentioned by Brongniart (1822a) under *Phyllites* was validly published there, neither can be regarded as the generic type, and an alternative must therefore be designated (ICN, Art. 38.2).

Nevertheless, the principle behind Andrews' (1955) suggestion makes considerable sense: Brongniart (1822a) clearly stated that his "*Phyllites populinus*" was the only species that was fully compatible with *Phyllites* and he used the specimen that he figured under that illegitimate species name to characterise the genus. This species was subsequently transferred to the extant genus *Populus* L. by Knobloch (1964); but, as pointed out by Doweld (2017b), the resulting combination (*Populus populina* (Brongniart) Knobloch, 1964) was pre-dated by *Populus populina* Jarmolenko, 1935 and thus illegitimate. There is, however, another previously published species (*Populus latior* A.Braun, 1845) that has very similar-shaped leaves to Brongniart's (1882a) "*Phyllites populinus*" specimen and originated from the same locality (the Miocene Lagerstätte at Öhningen, Switzerland). Since both the original Brongniart specimen of "*Phyllites populinus*" and the Braun (1845) type of *P. latior* are lost, Doweld (2017b) proposed as neotype for both species the same specimen, which also originated from Öhningen. As a consequence *P. populinus* becomes a later homotypic ("nomenclatural") synonym of *P. latior*, and so we propose here that *P. latior* should be regarded as the type of *Phyllites*.

Poacites Schlotheim ex Brongniart nom. illegit.

Text-fig. 2i

1820 *Poacites* Schlotheim, p. 416 (nom. inval.).
1822a *Poacites* Schlotheim ex Brongniart, p. 210 (nom. illegit.).

Type. *Poacites carinata* Brongniart, 1822a, p. 238, pl. 3, fig. 2; Loc.: Pennsylvanian Subsystem.

Diagnosis. "Feuilles linéaires, à nervures paralléles."

Discussion. This generic name was first used by Schlotheim (1820) for fossils he interpreted as being of grass-like leaves but this is invalid as it pre-dated the starting point for taxonomic nomenclature of fossil plants (ICN, Art. 13.1) as well as lacking a generic diagnosis (ICN, Art. 39.1). However, a review of Schlotheim's (1820) work by Ballenstedt (1821) mentioned one of the species, "*Poacites zeaeformis*" Schlotheim, accompanied by a brief description: "auf Tafel XXVI [of Schlotheim 1820] zwei Abbildungen von *Poacites zeaeformis*, welche Grasart mit dem Mais sehr viel Ähnlichkeit hat, verzüglich auf den selteren Exemplaren die noch Stengelblaettern zeigen." Since this review only mentioned this one species under the generic name *Poacites*, this species diagnosis may also be used for the genus (ICN, Art. 38.5), thereby validating the publication of the generic name in this review. Nevertheless, the name is in practice unusable as the syntypes (as illustrated in Schlotheim 1820: pl. 26, figs 1, 2) show different types of fossils and the diagnosis is effectively meaningless in identifying a species.

Apparently unaware of Ballenstedt's (1822) review, Brongniart (1822a) later illegitimately used the generic name *Pothocites* for a rather different, grass-like fossil, which he named *Pothocites carinata* Brongniart. This looks remarkably like a Carboniferous arborescent lycopsid leaf that today is usually named *Cyperites bicarinata* Lindley et Hutton, 1832 (e.g. compare with Rex 1983). Although Brongniart (1822a) does not refer to any of the four species described by Schlotheim (1820), he unequivocally attributed the generic name *Poacites* as he used it to Schlotheim and provided generic a diagnosis very similar to that of *Poacites* Schlotheim ex Ballenstedt. However, *P. carinata* is quite different from Schlotheim's types of *Poacites* and it would be difficult to see how both could be meaningfully included within the same fossil-genus. *Poacites* Schlotheim ex Brongniart should therefore be regarded as a later homonym of *Poacites* Schlotheim ex Ballenstedt and therefore regarded as illegitimate.

Palmacites Schlotheim ex Brongniart

Text-fig. 2c

1820 *Palmacites* Schlotheim, p. 393 (nom. inval.).
1822a *Palmacites* Schlotheim ex Brongniart, p. 210.

Type. *Palmacites lamanonis* Brongniart, p. 238, pl. 3, fig. 1; MNHN.F.1931.1; Loc.: Miocene Series, Aix-en-Provence, France.

Diagnosis. "Feuilles flabelliformes."

Discussion. Schlotheim (1820) originally used this genus name for a series of fossils that he regarded as belonging to palms. Most were Palaeozoic lycopsid stems, although one unillustrated species (*Palmacites flabellatus* Schlotheim, 1820, nom. inval.) was based on Jurassic fossils. Martius (1822) also referred to two of Schlotheim's species (*Palmacites obsolutus* Schlotheim and *Palmacites annulatus* Schlotheim) but again without providing a generic diagnosis.

In its validly published protologue, Brongniart (1822a) restricted the fossil-genus to flabelliform, palm-like foliage and referred to just one species that may be taken as the type, *P. lamonensis* (in the second, 1822b, c part of the paper he mentioned a second species, *Palmacites parisiensis* Brongniart but this post-dates the protologue). Brongniart (1828a: 120) later also included stems that he regarded as having palm affinities, and Sternberg (1825) included disseminules thought to be from palms (*Palmacites noeggerathii* Sternberg, 1825 – in fact Palaeozoic medullosalean disseminules). Nowadays, however, the name is usually used in Brongniart's (1822a) original sense for fabelliform, palm-like leaves (Read and Hickey 1972).

Carpolithes Schlotheim ex Brongniart nom. illegit.

Text-fig. 2g

1820 *Carpolithes* Schlotheim, p. 418 (nom. inval.).
1822a *Carpolithes* Brongniart, p. 210 (nom. illegit.).

Type. *Carpolithes thalictroides* Brongniart, 1822b, p. 61, pl. 3, fig. 5; Loc.: upper Oligocene Calcaire de Beauce, Paris Basin, France; ≡ *Stratiotes thalictroides* (Brongniart) Chandler, 1923.

Diagnosis. "Fruits ou semences."

Discussion. The complex nomenclatural history of this genus has been summarised by Wang (2011), who pointed out that there were a number of 18th and very early 19th century records of fossil disseminules as *Carpolithus*, but they predate the starting point for palaeobotanical nomenclature and so are invalid. The most widely quoted was when Linnaeus (1768: 172) referred to "*Phytolithus fructus*" as *Carpolithus*, but it is far from clear that he intended it as a generic name: he did not use it as part of a binomial, and it was not listed in the *Index Generum Lapidum* towards the end of the book.

The earliest validly published name that was intended for such fossils was *Carpolithes* Brongniart 1822a, the spelling of which had been based on the earlier but invalid *Carpolithes* Schlotheim, 1820, who used the name for a range of disseminule-like fossils of different ages. The name *Carpolithes* Brongniart had been used marginally earlier in Cuvier (1822) in combinations *Carpolithes thalictroides* var. *parisiensis* Brongniart, *Carpolithes thalictroides* var. *websteri* Brongniart and *Carpolithes ovulum* Brongniart, but neither genus, species nor variety names were accompanied by diagnoses and so were not validly published here; based on the same argument used earlier in the present paper in the section dealing with *Phyllites*, we cannot accept these as "illustration with analysis" that could validate the publication of the names under ICN, Art. 38.9 (the fossils had also been documented earlier by Alexander Brongniart, 1810: 382, pl. 23, figs 16, 17, but without name). The earliest validly published binomial that was accompanied by diagnosis was *C. thalictroides* Brongniart, 1822b; Brongniart (1822b) also mentioned *Carpolithes ovulum*, but only as a name in the caption for his pl. 6, fig. 2, without diagnosis or any other comment, and so was not validly published there. Consequently, as the first validly published species name to be combined by Brongniart with the generic name *Carpolithes*, *C. thalictroides* may be taken as the indicated type. However, as that species is the seed of an Oligocene aquatic angiosperm of the extant genus *Stratiotes* Linnaeus, 1753 (Chandler 1923), *Carpolithes* Brongniart was a later illegitimate taxonomic synonym of *Stratiotes* and should be supressed.

It might be queried if the diagnosis provided by Brongniart (1822a, b) was sufficient to distinguish *Carpolithes* from other taxa and therefore validated the publication of that name; it certainly provides few distinguishing characters. However, it is evident that Brongniart (1822a, b) had intended the genus to be used for any isolated fossil fruit or seed of uncertain affinities, and so in this context it does act as an effective diagnosis; *Carpolithes* Brongniart, 1822a was therefore validly published.

"*Carpolithus Mantellii*" was mentioned in a paper by Mantell (1824: 423, pl. 46, figs 3–4) but with no proper diagnosis; it is stated that there are "…veins on its surface…" but the fossils were not described or any indication given of how these "veins" distinguished the fossil from other species (although one of the figures is a close-up of the ovule, this is insufficient to merit designation as "illustration with analysis" that might validate the publication of the name). This species is usually attributed to C. Stokes and P. B. Webb, but their names are not mentioned in the paper, and the fossil is now regarded as an *Equisetum* Linnaeus, 1753 tuber rather than a disseminule (Watson and Batten 1990). The earliest validly published use of the name was *Carpolithus* Artis, 1825, based on a Pennsylvanian-age disseminule from Yorkshire, UK (type and only described species *Carpolithus marginatus* Artis, 1825). Wang (2011) suggested that Artis was merely adopting Brongniart's (1822a, b) *Carpolithes*, but Artis did not say this and it is notable that he used this quite different spelling to that of Brongniart (for the other taxa, Artis rigorously maintained the spelling used by the earlier authors). It therefore appears that the earliest published valid name for the fossil-genus envisaged by Brongniart (1822a) for fossil disseminules of uncertain affinities (and which is still widely used today – e.g. Crookall 1976) is *Carpolithus* Artis, 1825.

Antholithes Schlotheim ex Brongniart

Text-fig. 2h

1822a *Antholithes*, Brongniart, p. 210.

Type. *Antholithes liliacea* Brongniart, 1822a, p. 239, pl. 3, fig. 7; Loc.: Eocene Monte Bolca Lagerstätte in Veneto, Italy.

Diagnosis. "Fleurs."

Discussion. The species name *Antholithes liliacea* was not mentioned in the body of the text of Brongniart (1822a), its first mention being in Brongniart (1822b: 62). However, it was given in the caption for plate 3 in Brongniart (1822a). Although this was not accompanied by a specific diagnosis, as it is the only species in the fossil-genus *Antholithes*, following ICN, Art. 38.5 the generic diagnosis in Brongniart (1822a) may be taken also to validate the species name.

The type (Brongniart 1822a) appears to be a small bud-like structure, which Brongniart believed to be the perianth of a liliaceae-like flower. However, this is difficult to verify from the illustration and the location of the specimen is now unknown. In view of the generalised (albeit valid) diagnosis and the absence of a type, although it is validly published, it is difficult to see how the name *Antholithes* can be used in any meaningful way.

Concluding remarks

The Brongniart (1822a–c) paper forms the bedrock on which much of present-day palaeobotanical taxonomic nomenclature is built – both conceptually and in providing protologues of several widely used fossil-genera. Of the 24 generic / section names that he included in the "Classification", seven must be supressed as illegitimate or invalid, or have

been formally rejected (*Exogenites*, *Clatharia*, *Sagenaria*, *Filicites*, *Phyllites*, *Poacites*, *Carpolithes*), and four others are difficult to use because of problems with typification and / or diagnosis (*Endogenites*, *Culmites*, *Fucoides*, *Antholithes*). But most of the other 13 generic / section names are still in widespread use especially with Palaeozoic floras, albeit sometimes with slightly altered orthographies (*Calamites*, *Syringodendron*, *Sigillaria*, *Stigmaria*, *Sphenopteris*, *Neuropteris*, *Pecopteris*, *Odontopteris*, *Sphenophyllum*, *Palmacites*); or through conservation for other genera (*Lycopodites*, *Glossopteris*, *Asterophyllites*).

However, this analysis has shown that there are still problems with applying the ICN to palaeobotanical taxonomy. These largely arise from the tension between wanting to have an inclusive scheme that allows as many fossils as possible to be named and classified; and a scheme that maximises the taxonomic resolution using as much of the scientific data as possible. The Brongniart (1822a, b) scheme clearly falls into the former category, most modern palaeobotanical taxonomies the latter. Many palaeobotanists continue to use Brongniart's taxa (especially the fossil-genera) in the same way as he intended, especially for the less well understood fossils, whilst at the same time using more refined taxa based on features such as reproductive structure or internal anatomy for the better known species. This is not always permissible following the ICN: if the type of one of Brongniart's fossil-genera becomes better known and can be placed in one of these more narrowly defined fossil-genera, Brongniart's name must go with this latter genus, potentially resulting in many species becoming orphaned. To avoid this Jongmans et al. (1935) suggested that the Brongniart genera should be regarded as qualitatively different from "normal" botanical taxa, without types, but this was not adopted as part of the ICBN / ICN. Other potential solutions would be to create new "artificial" fossil-genera, to use a form of open nomenclature such as is often used in palaeozoology (e.g. Matthews 1973, Bengtson 1988), or to simply make taxonomic judgements on less than perfect evidence. In an ideal world we would all use the same approach but that is probably unrealistic. The best we can probably hope for is that taxonomists make it clear exactly what they are meaning when they use particular taxonomic names.

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